Survival strategies of a frugivore, the sun bear, in a forest-oil palm landscape

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Abstract

As large areas of forest are lost throughout the tropics, prime habitat of many species decline and become fragmented. The island of Borneo is a prime example, with accelerated clearing of forests primarily for oil palm expansion. Borneo's forests are an important stronghold for the conservation of the sun bear (*Helarctos malayanus*), but it is unclear how habitat reduction and fragmentation is affecting this frugivore. We used camera traps and sign surveys to understand patterns of sun bear habitat use in a matrix of fragmented forests and extensive oil palm development, which has existed as such for >15 years: the Lower Kinabatangan floodplain in Sabah, Malaysian Borneo. Within these small forest fragments, squeezed between a major river and oil palm plantations, bears exhibited selection for areas farther from human activity (forest edges, river boat traffic, and buildings), and were rarely active during the day, demonstrating both spatial and temporal avoidance of potential human-related threats. They selected large trees to feed and rest, and also exploited adjacent plantations to feed on oil palm fruits. We conclude that even relatively small forest fragments (~2,000 ha) within large agricultural landscapes can be important for sun bears. Our research highlights the remarkable adaptations this species has employed to persist in a drastically modified landscape.

Keywords: Borneo, Sabah, Lower Kinabatangan, oil palm, fragmentation, *Helarctos malayanus*, habitat use

1. Introduction

The island of Borneo has recorded high rates of forest loss (>30%) over the last four decades (Gaveau et al. 2014). In particular, the State of Sabah (Malaysian Borneo) alone lost nearly 40% of natural forest cover in that time (Gaveau et al. 2014). Agricultural expansion, which has been mostly for oil palm plantations, is one of the primary drivers behind forest loss, fragmentation, and degradation in the region (Koh and Wilcove 2008; Abram et al. 2014, 2016). The resulting pockets of forest stand out as islands amid a sea of monoculture (Ancrenaz et al. 2004; Abram et al. 2014). Although these forests may not be pristine in floral and faunal composition, they still may have tremendous value for biodiversity (Maddox et al. 2007; Alfred et al. 2012; Estes et al. 2012; Nakashima et al. 2013; Ancrenaz et al. 2015; Abram 2016).

Forested landscapes in Borneo are important for the continued survival of the sun bear (*Helarctos malayanus*)), a species whose range is limited to mainland Southeast Asia, Sumatra, and Borneo. Being a forest-dependent species, sun bears are adversely affected by excessive forest loss (Wong et al. 2013), but can survive in secondary or degraded forests provided that important habitat resources such as fruiting trees are available (Wong et al. 2004; Linkie et al. 2007; McShea et al. 2009; Samejima et al. 2012; Fredriksson 2012; Wong and Linkie 2013; Yaap et al. 2016; Wearn et al. 2017) Although sun bears consume insects (especially bees, beetles, and termites), both in trees and on the ground, most studies indicate that they are primarily frugivorous, unless fruits are scarce (McConkey and Galetti 1999; Augeri 2005; Cheah 2013; Steinmetz et al. 2013). In primary forests, the availability of sun bear food resources is tied to dipterocarp mast-fruiting cycles (Wong et al. 2005; Fredriksson et al. 2006). During inter-mast

periods, sun bear food sources become scarce, leading to starvation (Wong et al. 2005), greater predation risk (Fredriksson 2005a), and increased human–bear conflicts (Fredriksson 2005b; Wong et al. 2015).

With widespread deforestation and forest degradation occurring in Borneo, little is known about how sun bears have been responding to the extreme changes in their habitat. Research on other bear species in human-modified landscapes have shown them to be highly adaptable, supplementing their diet with crops (Maddrey and Pelton 1995; Charoo et al. 2011; Northrup et al. 2012; Takahata et al. 2014; Ditmer et al. 2015; Ali et al. 2017) while also attempting to minimize contact with people (Nielsen et al. 2004a; Ordiz et al. 2011). However, as bears use such landscapes more frequently, encounters between people and bears increase, representing increased risks for both species (Nielsen et al. 2004b; Jorgenson and Sandoval-A 2005; Charoo et al. 2011; Northrup et al. 2012; Scotson et al. 2014).

Our goal was to better understand the effects of the oil palm–forest landscape on sun bears, which might serve as an indicator for other, less-studied frugivores and carnivores (Ratnayeke and Van Manen 2012). We used two methods, camera trapping and sign surveys, both of which have been commonly used to study populations of bears in tropical regions (Akhtar et al. 2004; Ríos-Uzeda et al. 2007; Steinmetz 2011; Steinmetz et al. 2011; Ramesh et al. 2012; Sethy and Chauhan 2016)

Camera traps have become a standard tool for monitoring low-density large mammals in Southeast Asian forests (Kawanishi and Sunquist 2004; Linkie et al. 2007; Ngoprasert et al. 2012; Rayan et al. 2012; Wong et al. 2013; Wong and Linkie 2013), and have provided valuable information about mammalian use of the forest–oil palm plantation interface (Yue et al. 2015; Wearn et al. 2017). Camera trap studies of sun bears have yielded density estimates (Ngoprasert

et al. 2012), measures of habitat use and distribution (Wong et al. 2013; Wong and Linkie 2013), and assessments of activity patterns (Wong et al. 2004; Cheah 2013). Sign surveys within strip transects have also been used to assess the status of sun bear populations (Augeri 2005; Steinmetz et al. 2011, 2013; Ngoprasert et al. 2011; Fredriksson 2012). Sign surveys are useful as a measure of bear presence, relative abundance, and habitat use (Steinmetz and Garshelis 2010). We employed both these methods in our study to understand the strategies used by sun bears living in fragmented landscapes. Specifically, we wished to learn whether sun bears could effectively utilize remnant forest surrounded by expansive oil palm plantations, and if so, we sought to understand features of this habitat that they used or avoided, and aspects of their behavior that enabled them to survive there.

2. Materials and Methods

2.1 Study site

Our study site was situated in the Lower Kinabatangan floodplain, in the eastern part of Sabah, Malaysian Borneo. This area is dominated by oil palms, with only small forest fragments remaining (Abram et al. 2014). A network of protected areas consists of seven variably sized forest reserves as well as the Lower Kinabatangan Wildlife Sanctuary (LKWS), which itself constitutes ten different forested areas labelled as lots (Ancrenaz et al. 2004). Forest fragments that are currently protected have remained relatively unchanged since 1998 (~15 years at the time of this study; Francis et al., unpublished data). We surveyed five lots (numbered 1 and 4 – 7), four forest reserves (Keruak, Bod Tai, Gomantong, and Pin Supu), and private lands within the floodplain. Besides sun bears, large mammal species present in the landscape include the Bornean orangutan (*Pongo pygmaeus*), Asian elephant (*Elephas maximus*), proboscis monkey (*Nasalis larvatus*), and Sunda clouded leopard (*Neofelis diardi*).

115 2.2 Data collection

116 2.2.1 Habitat use

117 We used the detection of sun bears through camera traps as a primary measure of bear
118 habitat use in the Lower Kinabatangan. The primary goal of the camera trapping was to estimate
119 the density of Sunda clouded leopards in the region. As such, the location and method of
120 deployment was done to maximize the detections of clouded leopards; sun bear photos were non-
121 target data. We deployed Reconyx PC800 and HC500 infrared camera traps (Reconyx Inc.,
122 Holmen, Wisconsin, USA) at 77 different sites along riparian trails, forest trails, and ridgelines
123 (Figure 1). We secured camera traps to trees, 40–50 cm off the ground, with an average distance
124 of 1.22 km between adjacent sites (Ross et al. 2013). Cameras recorded the time and date of
125 every photographic capture. We checked camera sites at intervals of 30–80 days to check their
126 condition, replace batteries, and change memory cards. For each camera site, we divided the
127 sampling period into 44 weekly occasions from June 2013 until April 2014. Each occasion
128 represented a sun bear detection (1) or non-detection (0) event. We only considered independent
129 detections at each site, which we defined as photographs at least 24 hours apart.

130 We used the detection of sun bear sign as a second measure of bear habitat use. Sun bears
131 leave conspicuous and distinctive sign during foraging and resting events: claw marks on trees,
132 tree nests, ripped open logs, and broken termite nests (Fredriksson 2012; Steinmetz et al. 2013).
133 During 2012 – 2013, we searched for sign within 50 strip transects in the LKWS Lot 5 riparian
134 corridor and Lot 6 forest fragment (Figure 2). The riparian corridor is a relatively thin strip (130
135 m– 2 km width) of forest along the Kinabatangan River and connects LKWS Lot 7 and Pin Supu
136 Forest Reserve (together 3,723 ha) with the larger Lot 5 forest block and Gomantong Forest
137 Reserve (together approximately 11,900 ha; Ancrenaz et al. 2004)). Our transects were 0.25 ha in

size (5 x 500 m) and spaced at least 250 m apart, with 20 transects in the corridor and 30 in the fragment. Every tree within the transect was closely examined for claw marks, and the ground was searched for digging. On every survey, one leader trained in bear sign identification was present.

When we found bear claw marks on trees, we further distinguished between within-year and older claw marks based on our understanding of how marks age (Steinmetz and Garshelis 2010; Fredriksson 2012), measured the circumference at breast height (CBH) of the tree, identified the tree to family (or lower taxon where possible), and recorded if there were ripped open cavities or torn bark (indicating insect feeding; Fredriksson 2012). We noted if the transect contained signs of human activity (cut trails, campsites, rubbish, etc.) and counted the number of *Ficus sp*. trees and termite nests, both important food items for sun bears (Wong et al. 2002; Fredriksson et al. 2006; Fredriksson 2012), in each transect. Also, for comparative purposes, we searched an additional four 5 x 100 m (0.05 ha) transects in an area known to have abundant sun bear sign. These transects were within Pin Supu Forest Reserve (Figure 2), but close (80–320 m) to oil palm plantations. We selected this area after a farmer reported he had come across a sun bear in oil palm plantation bordering the reserve.

We considered six landscape covariates, deemed as potentially important determinants of sun bear habitat use: forest type, elevation, buildings, roads, intact forest edge, and water bodies. For forest type data, we modified existing forest type and land use cover information from 2010/11 data (Abram et al. 2014). We did this by updating the forest extent vector layer, in ArcMap 10.3 (Esri, Redlands, California, USA), using a 15 m resolution Landsat image from 2013, then extracted forest type information for the 2013 forested area. Roads included both surfaced highways and certain plantation roads; buildings represented all structures visible

(houses, storage areas, mills etc); and water bodies encompassed all rivers and oxbow lakes. All these features were digitized from SPOT 2.5 m 2010/11 satellite imagery. For each camera trap and strip transect, we measured the distance to the nearest building (hereafter building), intact forest edge (hereafter forest edge), road, and water body. For camera traps, we calculated the elevation and categorized the forest type as either freshwater swamp forest, mixed dipterocarp forest, limestone forest, or degraded scrub forest. For strip transects, we calculated the mean elevation of the start and end points of each transect.

2.2.2 Activity patterns

We used the time stamp on camera-trap photographs to examine the activity patterns of bears. For this dataset, we also included additional data from LKWS Lot 5 (10 sites; 2011 – 2015) and Lot 6 (7 sites; 2010 – 2011), which were set as part of a general biodiversity survey.

2.2.3 Climbed tree characteristics

We compared features associated with claw-marked trees to a sample of trees that sun bears did not climb. We randomly selected 48 claw marked trees from our strip transects as targets for further investigation. We then selected another 48 unclimbed trees for comparison. We chose these from transects lacking claw-marked trees: first by dividing the transect into five 100-m segments, and then searching each segment for a tree of suitable size for bears to climb (minimum CBH $\geq$ 29 cm based on data from this study).

We set up 20 x 20-m plots centered on each of the 48 climbed and 48 unclimbed trees. We measured the CBH and estimated the height of the focal tree using a clinometer. Within the plot, we counted the number of vines present (hereafter vines). For other habitat variables, we first divided each plot into four 10 x 10-m subplots. Two observers used a striped density stick to

quantify the percent understory density in each subplot. We used the mean of all subplots as a measure of the plot understory density. We photographed the canopy directly overhead at the center of each subplot and used the software "HabitApp" (Macdonald and Macdonald 2016) to calculate the proportion of the color black in the photo. Larger proportions indicated greater cover. We took the mean of these proportional values as the canopy cover for the plot.

2.3 Data analysis

2.3.1 Habitat use

We conducted all analysis using R (R Core Team 2015). We utilized a single season occupancy model to measure sun bear habitat use (ψ) from camera trap data (MacKenzie et al. 2002). We examined the effects of covariates (building, forest edge, water body, elevation, road, and forest type) on both ψ and detection probability (probability of a sun bear being detected during an occasion given that it is present; p) using the package "unmarked" (Fiske et al. 2011). In addition, we examined whether the number of trap nights a camera trap was operational in a weekly sampling occasion (0-7 trap nights) had an effect on p. We used Pearson's correlation coefficient (r_p) to check for multicollinearity among covariates ($r_p \geq 0.7$). We did not fit models with more than one covariate for ψ and two covariates for p to avoid overfitting the model. We began by fitting constant and single covariate models for both ψ and p. We fit two parameter models for p by taking covariates from the best ranked single covariate models ($\Delta AIC \leq 2$) and using these in combination with other covariates. The best supported models were identified based on Akaike's Information Criterion (AIC) and model weight. To identify competing models, we ignored models that were similar to a better ranked model but with an extra

parameter (Arnold 2010). We further assessed model fit through parametric bootstrap goodness of fit tests using the model sum of squared errors.

From our strip transect detection/non-detection data, we checked if the number of transects containing within-year sun bear sign and evidence of human activity differed between the corridor and forest fragment using chi-squared and Fisher's exact tests, respectively. We checked for differences in number of *Ficus sp.* trees, climbed tree CBH, and density of within year sign between transects in the corridor and fragment using Wilcoxon-Mann-Whitney tests.

We used logistic regression to model the presence of within-year sun bear sign in the Lower Kinabatangan. As the age of sign could only be reliably ascertained for claw marks on trees, we did not include other bear signs in this analysis. We did not include data from the four transects purposefully located in an area with high sign density. Our suite of covariates included building, road, forest edge, water body, elevation, number of *Ficus sp.* trees in a transect (hereafter *Ficus*), presence of human activity in a given transect (0 or 1), and transect location (corridor or fragment). We checked for multicollinearity among covariates ($r_p \geq 0.7$). We fit models with single covariates first, ranked them using AIC corrected for small sample sizes (AIC_c), and then fitted more complex models with covariates from the top ranked models ($\Delta AIC_c \leq 2$). We repeated this until we identified the best ranked models using AIC_c and model weight. We ignored competing models with only one additional parameter to better supported models (Arnold 2010). We inspected the fit of the top ranked models visually using binned residual versus fitted plots. Lastly, we used the area under the receiver operating characteristic (ROC) curve to assess the predictive power of the best supported models.

2.3.2 Activity patterns

We used the R package "overlap" (Meredith and Ridout 2014) to calculate a kernel density function from times at photographic capture of sun bears in the Lower Kinabatangan during 2010-2015. For this analysis, we only used independent detections (one detection at a site 24 hour^{-1}) of bears.

2.3.3 Climbed tree characteristics

We used Wilcoxon-Mann-Whitney tests to check for differences in understory density, canopy cover, tree height, vines, and CBH between climbed and non-climbed tree plots as well as between trees with within-year claw marks and those without. We used logistic regression to model the habitat characteristics most associated with climbed trees. We ran two groups of models: one with the response being the presence or absence of claw marks on a tree and another with the response being the presence or absence of within-year claw marks on a tree. We used six covariates in total: CBH, tree height, canopy cover, understory density, vines, and location. We checked for correlation among predictors ($r_p \geq 0.7$). We fit models sequentially with single covariates first and then adding predictors from the top ranked models ($\Delta AIC_c \leq 2$). The final suite of best supported models were selected and assessed similarly to the habitat use analysis.

3. Results

3.1 Habitat use

We obtained 583 photographs of sun bears from 11,359 camera trap nights in the lower Kinabatangan. From these, only 59 represented independent detections according to our criteria (192.5 trap nights/independent detection of a sun bear). We detected sun bears at 29 of 77 (38%) camera trap sites.

The best ranked single season occupancy model included ψ as constant and *p* as a function of forest edge and building (Table 1). The parametric bootstrap goodness of fit test using the model sum of squared errors suggested a good fit for this model (P = 0.37). Our best estimate of ψ was 0.74 (SE = 0.12). Detection of sun bears on camera traps increased farther from buildings and farther from the forest edge (i.e., more interior; Figure 3). Our best estimate of *p* was 0.03 (SE = 0.01) at the mean distance to building (2.08 km) and forest edge (0.61 km). The probability of detecting a sun bear throughout the entire survey (all 44 weekly occasions; *p**) was 77.6% at the mean covariate values.

We detected sun bear sign (96.8% claw-marked trees, 3.2% ripped open logs, n = 94) in 31 of 50 strip transects. In both the corridor and fragment, a large proportion of transects contained sign (60% and 70%, respectively). All ripped-open logs (insect feeding) were within the fragment transects. Of the 91 claw-marked trees that we observed, about half (48.4%) were judged to have been made within 1 year. The density of within-year bear claw marks was higher in the fragment (median = 4 ha^{-1}, SD = 6.33 ha^{-1}) than the corridor (median = 0 ha^{-1}, SD = 3.0 ha^{-1}), but this difference was not significant (P = 0.17). All four transects in the Pin Supu Forest Reserve contained bear sign, and sign density was extremely high (median = 100 ha^{-1}, SD = 60.0 ha^{-1}).

Six tree families made up 67% of the total climbed trees found on sign survey transects: Sterculiaceae, Lamiaceae, Lauraceae, Euphorbiaceae, Rubiaceae, and Tiliaceae. Climbed trees in the corridor were smaller ($\bar{x}$ = 132.1 cm, SD = 75.1 cm) than trees in the fragment ($\bar{x}$ = 145.5 cm, SD = 107.2 cm) but this difference was not significant (P = 0.94). About a quarter (26.4%) of the climbed trees had torn bark or holes that were noticeable, consistent with sign of insect feeding by a bear. In terms of other potential bear food sources, we located 71 *Ficus sp.* trees and

4 termite mounds within transects. A larger number of *Ficus sp.* trees per transect were in the corridor ($\bar{x}$ = 2.55, SD = 3.86) than in the fragment ($\bar{x}$ = 0.6, SD = 0.81; P = 0.03). All termite mounds were within the fragment. Corridor transects were more disturbed (59.3% contained human signs) than fragment transects (40.7%; P = 0.004).

Building, elevation, and water were significant predictors of within-year sun bear sign (Table 2). Greater distances from buildings and water, and higher elevations were associated with higher detection of within-year claw marks (Figure 4). All competing models had moderate predictive power (61–72%). Binned residual versus fitted plots of competing models displayed an acceptable fit.

3.2 Activity patterns

We obtained 953 photographs of sun bears during 2010–2015, of which 116 were independent detections according to our criteria. On trails and ridgelines, bears were largely crepuscular with sustained nocturnal activity (Figure 5). Sun bear activity peaked at around 2000 and again at 0400 hours, with a low activity during daylight, especially between 0800 and 1600 hours.

3.3 Climbed tree characteristics

Considering bear claw marks of all ages, we found that understory density and number of vines around climbed trees was less than around unclimbed trees (Table 3). Climbed trees were also taller and had a larger CBH (Table 3). When considering only trees climbed by bears that year, we detected similar selections by bears for tress with less understory density that were taller and that had a larger CBH (Table 4).

293 The best supported model explaining climbed tree selection contained the covariates
294 understory density and height (Table 5). Tree height was positively associated with climbed trees
295 while understory density seemed to have a negative impact on tree climbing (Figure 6). The
296 binned residual versus fitted plots showed good fit, and the model had high predictive power
297 (89.2%). For models focused on just within-year marks, the probability of climbing increased
298 significantly (76%; best supported model) if the tree was within the fragment (Table 6). Tree
299 height and understory density were also significant covariates of within-year climbing. All top
300 ranked models explaining within-year climbing fit decently, and had good predictive power (76-
301 78.5%).

302 **4. Discussion**

303 Camera-trap detection rates of sun bears was moderately high in the Lower Kinabatangan
304 (1 bear detection every 192.5 camera trap nights) compared to other locations across mainland
305 Southeast Asia (Steinmetz 2011). One caveat of our study was that our camera traps were placed
306 solely on wildlife trails and ridgelines, limiting our inference to just these habitat features. Our
307 study suggested sun bears used many portions (74%) of the riparian trails, forest trails, and
308 ridgelines in the landscape. This high perceived use was likely due to the long survey period in
309 our study, enabling the accumulation of detections of a fairly wide-ranging species. In addition,
310 the sites were not closed (bears could have been present in the vicinity of a camera trap during
311 some weeks but not others) and the small area of forest left in the Lower Kinabatangan probably
312 confined bears to a limited space, hence they would use a large part of the remaining forest.
313 However, the lack of closure does not affect inferences about habitat use (MacKenzie et al.
314 2018). Therefore, we presume that the comparatively high habitat use estimate was the result of
315 the circumstances of the species and study, rather than a high density of bears.

316 We observed a decline in the probability of detecting bears closer to buildings, the forest
317 edge, and water bodies, all used frequently by people. Although our estimate of habitat use was
318 high, the intensity of use was drastically affected by a sensitivity towards human presence. This
319 has been observed elsewhere in the sun bear's range (Augeri 2005; Nazeri et al. 2012, 2014;
320 Wong and Linkie 2013). In contrast, forest streams not used intensively by people were reported
321 to attract sun bears (Nazeri et al. 2014). Our study clearly shows that sun bear habitat use in the
322 Lower Kinabatangan is driven by an avoidance to anthropogenic disturbance or threats.

323 Elevation appeared to be an additional predictor of sun bear habitat use, as reflected by
324 within-year sign, even though the difference in minimum and maximum elevations of our strip
325 transects was only 17 m. We suspect that bears were not actively selecting slightly higher
326 elevations, but rather habitat features associated with these elevations. Lower lying patches of
327 habitat become inundated and hold water more frequently, which may restrict sun bear use
328 directly and also may impact the composition of tree species and understory (Abram et al. 2014).

329 Sun bears have been recorded venturing past the forest edge to feed in oil palm
330 plantations (Normua et al. 2004; Cheah 2013; Yue et al. 2015; Wearn et al. 2017; Guharajan et
331 al. 2017). As the camera trap survey was not targeted directly at sun bears, we did not have
332 cameras placed within oil palm plantations, but sign surveys (see below) and reports from
333 farmers in the area (Guharajan et al. 2017), indicated that at least some sun bears fed in
334 plantations. Poachers use tree platforms and snares to hunt at the forest–oil palm interface (R.
335 Guharajan and S. Payar, pers. obs.). It is thus risky for bears to use trails crossing into the
336 agricultural lands. In addition, we do not know if lack of use of these trails during daylight hours
337 was indicative of their general activity pattern in the area, or just an avoidance of trails at times
338 when humans might have been present. Sun bears have been observed to be active mainly during

non-daylight hours in human-disturbed habitats (Mohd-Azlan 2006; Cheah 2013) but diurnal where human disturbance was low (Fredriksson 2012). In a different forest reserve in Sabah, radiocollared sun bears were diurnally-active in the forest, but bears were photographed on trails mainly during crepuscular-nocturnal hours (Wong et al. 2004).

Based on sign density, bears used the narrow riparian corridor (Lot 5), but they appeared to make greater use of the larger forest fragment directly across the river (Lot 6; Figure 2; Table S1). We found a higher density of *Ficus sp.* trees, an important food source and possible attractant, within corridor transects; however, even with a greater potential density of food in the corridor, sun bears showed an apparent wariness to the proximity of human disturbance, which occurred on both sides of the narrow corridor. Although the Lot 6 fragment is also relatively small (2,673 ha; Ancrenaz et al. 2004), it may provide more insulation from these anthropogenic disturbances.

The sign we observed, primarily claw-marked trees, was a more definitive indication than camera-trap photos that the forest patches provided resources to sustain bears, not just cover to pass through. Sun bears climb trees to feed on fruits and insects, for refuge while resting, and possibly to cool off from the hot and humid weather. Accordingly, their selection for larger trees may have provided (1) a higher density of fruits than smaller trees, (2) more cavities for insects like stingless bees (*Trigona* spp.), (3) larger branches for resting, and (4) better access for bears to get above the surrounding canopy where there might be breeze. Conversely, Powell (2011) found no selection by sun bears for taller trees in a more intact and diverse forest in Sumatra, possibly because this forest offered a greater abundance and diversity of fruiting trees, so bears could afford to seek a diet of assorted fruits (as shown empirically by Steinmetz et al. 2013). We also found that sun bears tended to climb trees surrounded by a sparser understory. The sparser

362 understory below these climbed trees is likely a reflection of a less-disturbed and more shaded
363 forest, rather than selection by sun bears for open understory per se.

364 We found exceedingly high sun bear sign density in a patch of forest within Pin Supu
365 Forest Reserve (110 within-year sign ha^{-1}; 135 all-aged sign ha^{-1}), near where a farmer reported
366 seeing bears foraging in oil palm. Elsewhere, others have reported sun bear sign densities of 4.9
367 – 8.8 all aged sign ha^{-1} in primary and commercial forests of central Sabah (Teo 2013), 40 – 45
368 all-aged sign ha^{-1} in prime habitat in Indonesian Borneo (Augeri 2005; Fredriksson 2012) and
369 only 9 within-year sign ha^{-1} in prime habitat in western Thailand (Steinmetz et al. 2011). The
370 high sign density in the small patch of Pin Supu Forest Reserve (~ 2,000 ha) suggests that bears
371 may have used it as a frequent refuge between feeding bouts into the plantations. Nighttime
372 feeding forays from the forest into oil palm plantations have been observed among radiocollared
373 bears at another site in Sabah (Normua et al. 2004) and Peninsular Malaysia (Cheah 2013).
374 Likewise, camera-trap photos elsewhere in Sabah showed that sun bears used both oil palm
375 plantations and the adjacent forest (Yue et al. 2015; Wearn et al. 2017). The high use of small
376 forest patches, like Pin Supu, Lot 5 and Lot 6, signify their importance for sun bears in the
377 Lower Kinabatangan.

378 **5. Conclusions**

379 Sun bears exhibited a clear avoidance, in both space and time, of humans in the Lower
380 Kinabatangan. This strategy is undoubtedly beneficial when living in a landscape dominated by
381 people and agricultural activities, where encounters with humans could be deadly. This strategy
382 also aids in the utilization of an important food resource: oil palm fruits. Sun bears do feed on
383 this easily available and abundant food source (Normua et al. 2004; Cheah 2013) but oil palm
384 workers and farmers in our study area hardly encountered bears, likely because the bears only

used these plantations at night (Guharajan et al. 2017). This highlights how this extremely adaptable frugivore is able to make use of beneficial resources in a degraded and potentially dangerous landscape. Encouragingly, camera-trapped sun bears in the lower Kinabatangan did not exhibit any gunshot wounds or snare-related injuries, unlike those from a similar landscape in Peninsular Malaysia (Cheah 2013). However, discoveries of disemboweled sun bear carcasses with missing paws in the landscape (L. Liman, WWF-Malaysia, pers. comm., T. Eriksson, pers. comm.) suggest that poaching of this species does occur, though the extent is still not clear. Our research indicates that sun bears can survive in a landscape like the Lower Kinabatangan for at least 15 years, provided there are pockets of connected forests: even small fragments that can serve as refuges and core areas. Additionally, 12 other carnivores were detected by the camera traps in the forest fragments where we worked, demonstrating the importance of saving even small forest remnants (Evans et al. 2016). Likewise, sun bears and other threatened species have been observed at reasonably high rates (via camera-trapping) in riparian forest fragments in Indonesia (Yaap et al. 2016). Whereas there are obviously severe negative impacts of widespread land conversion and fragmentation on this forest-dependent species, our results offer hope that conservation of forest fragments within the agricultural landscape enables this species, and others like it, to persist. We believe that the most pressing conservation action needed for sun bears in the Lower Kinabatangan is not to do with habitat or food resources, but protection from human-caused mortality, primarily poaching.

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7. Data availability

The datasets used in this study are available upon request from the corresponding author.

8. References

Abram NK (2016) Trade-offs between ecosystem protection and oil palm development. Royal Institution of Chartered Surveyors

Abram NK, MacMillan DC, Xofis P, et al (2016) Identifying where REDD+ financially out-competes oil palm in floodplain landscapes using a fine-scale approach. PLOS ONE 11:e0156481. doi: 10.1371/journal.pone.0156481

Abram NK, Xofis P, Tzanopoulos J, et al (2014) Synergies for improving oil palm production and forest conservation in floodplain landscapes. PLoS ONE 9:e95388. doi: 10.1371/journal.pone.0095388

Akhtar N, Singh Bargali H, Chauhan NPS (2004) Sloth bear habitat use in disturbed and unprotected areas of Madhya Pradesh, India. Ursus 15:203–211. doi: 10.2192/1537-6176(2004)015<0203:SBHUID>2.0.CO;2

Alfred, R., Ahmad, A.H., Payne, J., Williams, C., Ambu, L.N., How, P.M., Goossens, B., 2012. Home range and ranging behaviour of Bornean elephant (*Elephas maximus borneensis*) females. PLoS ONE 7, e31400. doi:10.1371/journal.pone.0031400

Ali A, Zhou Z, Waseem M, et al (2017) An assessment of food habits and altitudinal distribution of the Asiatic black bear (*Ursus thibetanus*) in the Western Himalayas, Pakistan. J Nat Hist 51:689–701. doi: 10.1080/00222933.2017.1303097

Ancrenaz M, Goossens B, Gimenez O, et al (2004) Determination of ape distribution and population size using ground and aerial surveys: a case study with orang-utans in lower Kinabatangan, Sabah, Malaysia. Anim Conserv 7:375–385. doi: 10.1017/S136794300400157X

438 Ancrenaz, M., Oram, F., Ambu, L., Lackman, I., Ahmad, E., Elahan, H., Kler, H., Abram, N.K.,
439 Meijaard, E., 2015. Of Pongo, palms and perceptions: a multidisciplinary assessment of
440 Bornean orang-utans *Pongo pygmaeus* in an oil palm context. Oryx 49, 465–472.
441 doi:10.1017/S0030605313001270

442 Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information
443 Criterion. J Wildl Manag 74:1175–1178. doi: 10.2193/2009-367

444 Augeri DM (2005) On the biogeographic ecology of the Malayan sun bear. PhD dissertation,
445 University of Cambridge

446 Charoo SA, Sharma LK, Sathyakumar S (2011) Asiatic black bear–human interactions around
447 Dachigam National Park, Kashmir, India. Ursus 22:106–113. doi: 10.2192/URSUS-D-
448 10-00021.1

449 Cheah, C.P.I., 2013. The ecology of Malayan sun bears (*Helarctos malayanus*) at the Krau
450 Wildlife Reserve, Pahang, Malaysia and adjacent plantations (PhD dissertation).
451 Universiti Putra Malaysia.

452 Ditmer, M.A., Garshelis, D.L., Noyce, K.V., Haveles, A.W., Fieberg, J.R., 2015. Are American
453 black bears in an agricultural landscape being sustained by crops? J. Mammal. 97, 54-67.
454 doi:10.1093/jmammal/gyv153

455 Estes JG, Othman N, Ismail S, et al (2012) Quantity and configuration of available elephant
456 habitat and related conservation concerns in the Lower Kinabatangan floodplain of
457 Sabah, Malaysia. PLoS ONE 7:e44601. doi: 10.1371/journal.pone.0044601

458 Evans MN, Vickers SH, Abu-Bakar MS, Goossens B (2016) Small carnivores of the Lower
459 Kinabatangan Wildlife Sanctuary, Sabah, Borneo, including a new locality for the otter
460 civet Cynogale bennettii. Small Carniv Conserv 54:26–38

461 Fiske I, Chandler R, others (2011) unmarked: An R package for fitting hierarchical models of
462 wildlife occurrence and abundance. J Stat Softw 43:1–23

463 Fredriksson, G.M., 2012. Effects of El-Nino and large-scale forest fires on the ecology and
464 conservation of Malayan sun bears (*Helarctos malayanus*) in East Kalimantan,
465 Indonesian Borneo (PhD dissertation). Universiteit van Amsterdam.

466 Fredriksson GM (2005a) Predation on sun bears by reticulated python in East Kalimantan,
467 Indonesian Borneo. Raffles Bull Zool 53:165–168

468 Fredriksson GM (2005b) Human-sun bear conflicts in East Kalimantan, Indonesian Borneo.
469 Ursus 16:130–137

470 Fredriksson, G.M., Wich, S.A., Trisno, 2006. Frugivory in sun bears (*Helarctos malayanus*) is
471 linked to El Niño-related fluctuations in fruiting phenology, East Kalimantan, Indonesia.
472 Biol. J. Linn. Soc. 89, 489–508.

473 Gaveau DLA, Sloan S, Molidena E, et al (2014) Four decades of forest persistence, clearance
474 and logging on Borneo. PLoS ONE 9:e101654. doi: 10.1371/journal.pone.0101654

475 Guharajan R, Abram NK, Magguna MA, et al (2017) Does the Vulnerable sun bear *Helarctos*
476 *malayanus* damage crops and threaten people in oil palm plantations? Oryx 1–9. doi:
477 10.1017/S0030605317001089

478 Jorgenson JP, Sandoval-A S (2005) Andean bear management needs and interactions with
479 humans in Colombia. Ursus 16:108–116. doi: 10.2192/1537-
480 6176(2005)016[0108:ABMNAI]2.0.CO;2

481 Kawanishi K, Sunquist ME (2004) Conservation status of tigers in a primary rainforest of
482 Peninsular Malaysia. Biol Conserv 120:329–344. doi: 10.1016/j.biocon.2004.03.005

483 Koh LP, Wilcove DS (2008) Is oil palm agriculture really destroying tropical biodiversity?: Oil
484 palm agriculture and tropical biodiversity. Conserv Lett 1:60–64. doi: 10.1111/j.1755-
485 263X.2008.00011.x

486 Linkie M, Dinata Y, Nugroho A, Haidir IA (2007) Estimating occupancy of a data deficient
487 mammalian species living in tropical rainforests: Sun bears in the Kerinci Seblat region,
488 Sumatra. Biol Conserv 137:20–27. doi: 10.1016/j.biocon.2007.01.016

489 Macdonald, G., Macdonald, H., 2016. HabitApp. Available at:
490 http://www.scrufster.com/habitapp/

491 MacKenzie DI, Nichols JD, Lachman GB, et al (2002) Estimating site occupancy rates when
492 detection probabilities are less than one. Ecology 83:2248–2255

493 MacKenzie DI, Nichols JD, Royle JA, et al (2018) Occupancy estimation and modeling:
494 inferring patterns and dynamics of species occurrence. Academic Press, London

495 Maddox, T., Priatna, D., Gemita, E., Salampessy, A., 2007. The conservation of tigers and other
496 wildlife in oil palm plantations, Jambi Province, Sumatra, Indonesia (October 2007).
497 Unpublished report. Zoological Society of London.

498 Maddrey RC, Pelton MR (1995) Black bear damage to agricultural crops in coastal North
499 Carolina. In: Proceedings of the Annual Conference of Southeastern Associated Fish and
500 Wildlife Agencies. pp 570–579

501 McConkey KIM, Galetti M (1999) Seed dispersal by the sun bear Helarctos malayanus in
502 Central Borneo. J Trop Ecol 15:237–241

503 McShea WJ, Stewart C, Peterson L, et al (2009) The importance of secondary forest blocks for
504 terrestrial mammals within an Acacia/secondary forest matrix in Sarawak, Malaysia. Biol
505 Conserv 142:3108–3119. doi: 10.1016/j.biocon.2009.08.009

506 Meredith, M., Ridout, M.S., 2014. overlap: Estimates of coefficient of overlapping for animal
507 activity patterns. Available at: https://CRAN.R-project.org/package=overlap

508 Mohd-Azlan J (2006) Mammal diversity and conservation in a secondary forest in Peninsular
509 Malaysia. Biodivers Conserv 15:1013–1025. doi: 10.1007/s10531-004-3953-0

510 Nakashima, Y., Nakabayashi, M., Sukor, J.A., 2013. Space use, habitat selection, and day-beds
511 of the common palm civet (*Paradoxurus hermaphroditus*) in human-modified habitats in
512 Sabah, Borneo. J. Mammal. 94, 1169–1178. doi:10.1644/12-MAMM-A-140.1

513 Nazeri, M., Jusoff, K., Madani, N., Mahmud, A.R., Bahman, A.R., Kumar, L., 2012. Predictive
514 modeling and mapping of Malayan sun bear (*Helarctos malayanus*) Distribution Using
515 Maximum Entropy. PLoS ONE 7, e48104. doi:10.1371/journal.pone.0048104

516 Nazeri M, Kumar L, Jusoff K, Bahaman AR (2014) Modeling the potential distribution of sun
517 bear in Krau wildlife reserve, Malaysia. Ecol Inform 20:27–32. doi:
518 10.1016/j.ecoinf.2014.01.006

519 Ngoprasert D, Reed DH, Steinmetz R, Gale GA (2012) Density estimation of Asian bears using
520 photographic capture–recapture sampling based on chest marks. Ursus 23:117–133. doi:
521 10.2192/URSUS-D-11-00009.1

522 Ngoprasert D, Steinmetz R, Reed DH, et al (2011) Influence of fruit on habitat selection of Asian
523 bears in a tropical forest. J Wildl Manag 75:588–595. doi: 10.1002/jwmg.83

524 Nielsen SE, Boyce MS, Stenhouse GB (2004a) Grizzly bears and forestry I. Selection of
525 clearcuts by grizzly bears in west-central Alberta, Canada. For Ecol Manag 199:51–65.
526 doi: 10.1016/j.foreco.2004.04.014

527 Nielsen SE, Herrero S, Boyce MS, et al (2004b) Modelling the spatial distribution of human-
528 caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. Biol Conserv
529 120:101–113. doi: 10.1016/j.biocon.2004.02.020

530 Normua F, Higashi S, Ambu L, Mohamed M (2004) Notes on oil palm plantation use and
531 seasonal spatial relationships of sun bears in Sabah, Malaysia. Ursus 15:227–231

532 Northrup JM, Stenhouse GB, Boyce MS (2012) Agricultural lands as ecological traps for grizzly
533 bears. Anim Conserv 15:369–377. doi: 10.1111/j.1469-1795.2012.00525.x

534 Ordiz A, Støen O-G, Delibes M, Swenson JE (2011) Predators or prey? Spatio-temporal
535 discrimination of human-derived risk by brown bears. Oecologia 166:59–67. doi:
536 10.1007/s00442-011-1920-5

537 Powell, V., 2011. Resource use and habitat utilization of Malayan sun bear (Helarctos
538 malayanus) in Harapan Rainforest, Sumatra (End of Project Report). Unpublished report.
539 International Association for Bear Research and Management.

540 R Core Team (2015) R: A language and environment for statistical computing. R Foundation for
541 Statistical Computing, Vienna, Austria

542 Ramesh T, Kalle R, Sankar K, Qureshi Q (2012) Factors affecting habitat patch use by sloth
543 bears in Mudumalai Tiger Reserve, Western Ghats, India. Ursus 23:78–85. doi:
544 10.2192/URSUS-D-11-00006.1

545 Ratnayeke S, Van Manen FT (2012) Assessing sloth bears as surrogates for carnivore
546 conservation in Sri Lanka. Ursus 23:206–217

547 Rayan, D.M., Mohamad, S.W., Dorward, L., Aziz, S.A., Clements, G.R., Christopher, W.C.T.,
548 Traeholt, C., Magintan, D., 2012. Estimating the population density of the Asian tapir
549 (*Tapirus indicus*) in a selectively logged forest in Peninsular Malaysia. Integr. Zool. 7,
550 373–380. doi:10.1111/j.1749-4877.2012.00321.x

551 Ríos-Uzeda B, Gómez H, Wallace RB (2007) A preliminary density estimate for Andean bear
552 using camera-trapping methods. Ursus 18:124–128. doi: 10.2192/1537-
553 6176(2007)18[124:APDEFA]2.0.CO;2

554 Ross J, Hearn AJ, Johnson PJ, Macdonald DW (2013) Activity patterns and temporal avoidance
555 by prey in response to Sunda clouded leopard predation risk: Activity of Sunda clouded
556 leopards and their prey. J Zool 290:96–106. doi: 10.1111/jzo.12018

557 Samejima H, Ong RC, Lagan P, Kitayama K (2012) Camera-trapping rates of mammals and
558 birds in a Bornean tropical rainforest under sustainable forest management. 270:248–256

559 Scotson L, Vannachomchan K, Sharp T (2014) More valuable dead than deterred? Crop-raiding
560 bears in Lao PDR. Wildl Soc Bull 38:783–790. doi: 10.1002/wsb.466

561 Sethy J, Chauhan NS (2016) Status and distribution of Malayan sun bear in Namdapha Tiger
562 Reserve, Arunachal Pradesh, India. Int J Conserv Sci 7:533–552

563 Steinmetz, R., 2011. Ecology and distribution of sympatric Asiatic black bears and sun bears in
564 the seasonally dry forests of Southeast Asia, in: W. McShea, S. Davies, and N.
565 Bhumpakphan (eds). The Ecology and Conservation of Seasonally Dry Forests in Asia.
566 Smithsonian Institution Press, Washington, D.C., pp. 249–273.

567 Steinmetz R, Garshelis DL (2010) Estimating ages of bear claw marks in Southeast Asian
568 tropical forests as an aid to population monitoring. Ursus 21:143–153

569 Steinmetz R, Garshelis DL, Chutipong W, Seuaturien N (2013) Foraging ecology and
570 coexistence of Asiatic black bears and sun bears in a seasonal tropical forest in Southeast
571 Asia. J Mammal 94:1–18. doi: 10.1644/11-MAMM-A-351.1

572 Steinmetz R, Garshelis DL, Chutipong W, Seuaturien N (2011) The Shared Preference Niche of
573 Sympatric Asiatic Black Bears and Sun Bears in a Tropical Forest Mosaic. PLoS ONE
574 6:e14509. doi: 10.1371/journal.pone.0014509

575 Takahata C, Nielsen SE, Takii A, Izumiyama S (2014) Habitat selection of a large carnivore
576 along human-wildlife boundaries in a highly modified landscape. PLoS ONE 9:e86181.
577 doi: 10.1371/journal.pone.0086181

578 Teo, S.D., 2013. Habitat use by Malayan sun bears (*Helarctos malayanus*) in the lowland
579 rainforests of Sabah, Malaysian Borneo (MSc thesis). National Pingtung University of
580 Science and Technology.

581 Wearn OR, Rowcliffe JM, Carbone C, et al (2017) Mammalian species abundance across a
582 gradient of tropical land-use intensity: A hierarchical multi-species modelling approach.
583 Biol Conserv 212:162–171. doi: 10.1016/j.biocon.2017.05.007

584 Wong ST, Servheen C, Ambu L, Norhayati A (2005) Impacts of fruit production cycles on
585 Malayan sun bears and bearded pigs in lowland tropical forest of Sabah, Malaysian
586 Borneo. J Trop Ecol 21:627–639. doi: 10.1017/S0266467405002622

587 Wong, S.T., Servheen, C.W., Ambu, L., 2004. Home range, movement and activity patterns, and
588 bedding sites of Malayan sun bears *Helarctos malayanus* in the Rainforest of Borneo.
589 Biol. Conserv. 119, 169–181. doi:10.1016/j.biocon.2003.10.029

590 Wong ST, Servheen CW, Ambu LN (2002) Food habits of Malayan sun bears in lowland
591 tropical forests of Borneo. Ursus 13:127–136

592 Wong W-M, Leader-Williams N, Linkie M (2013) Quantifying changes in sun bear distribution
593 and their forest habitat in Sumatra: Sun bear population trends and deforestation in
594 Sumatra. Anim Conserv 16:216–223. doi: 10.1111/j.1469-1795.2012.00587.x

595 Wong W-M, Leader-Williams N, Linkie M (2015) Managing human-sun bear conflict in
596 Sumatran agroforest systems. Hum Ecol 43:255–266. doi: 10.1007/s10745-015-9729-1

597 Wong W-M, Linkie M (2013) Managing sun bears in a changing tropical landscape. Divers
598 Distrib 19:700–709. doi: 10.1111/ddi.12020

599 Yaap B, Magrach A, Clements GR, et al (2016) Large mammal use of linear remnant forests in
600 an industrial pulpwood plantation in Sumatra, Indonesia. Trop Conserv Sci
601 9:194008291668352. doi: 10.1177/1940082916683523

602 Yue S, Brodie JF, Zipkin EF, Bernard H (2015) Oil palm plantations fail to support mammal
603 diversity. Ecol Appl 25:2285–2292

604